

**AN ETHOLOGICAL STUDY OF ANOPLIUS
(POMPILINUS) FRATERNUS (BANKS)
(HYMENOPTERA, POMPILIDAE).**

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The pompilid wasp *Anoplius (Pompilinus) fraternus* (Banks) was described originally in 1941, and until 1951 was known only from the type series of two females. It is still poorly represented in most collections. In a revision of the genus in 1951 Evans (Trans. Amer. Ent. Soc. 76: 322) redescribed the species from 85 specimens from various localities from Florida and Texas north to Long Island and to Nebraska. It was noted that nearly all the records were from sea beaches or inland salt flats. The species occurs occasionally on sandy beaches, often where there is seaweed or debris, but more frequently on muddy salt flats around salt marshes or salt lakes. Within its habitat it is often extremely abundant at the proper season. Its restriction to a habitat which is unusual for a pompilid undoubtedly accounts for its scarcity in collections.

During the springs of 1953 and 1954 we spent a few days on the salt flats at Cape Sable, Everglades National Park, Florida. The observations reported here were made near the southern terminus of the gravel road running through the Park, a place called Flamingo on many maps. The actual dates were March 31, 1953, and March 24, 25, and 27, 1954. The observations made in 1953 were reported briefly by Krombein and Evans in 1954 (Proc. Ent. Soc. Washington 56: 231). At this locality we encountered a very large population of *fraternus* which, judging from the uniformly fresh appearance of specimens and the abundance of males, must have emerged not more than a week or two prior to our arrival. Specimens were taken on debris at the ocean edge and, in much greater numbers, on bare spots and in the vegetation surrounding them on the salt flats behind the beach. The soil on the flats is heavy, black, and has a high salt content. The top crust tends to be hard and dry, but down to a depth of about 20-30 cm. it is somewhat moist, and below this depth it is saturated with water. In this habitat only two other species of Pompilidae were taken, and these in very small numbers. In fact, aside from *fraternus*, a large colony of *Bembix cinerea* Hand-

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lirsch, and considerable numbers of two species of Mutillidae, aculeate wasps were notably uncommon in this area. *Anoplius fraternus* and *Bembix cinerea* seem adapted for life in this type of habitat. The lack of competition, numerous nesting sites, and abundance of prey (spiders and horseflies, respectively) apparently enable these two species to build up high populations on the salt flats.

In the following summary of our notes on *fraternus* reference is made to the observers by the use of initials, and to the numbers of the field notes and associated specimens, which are on file at the writers' respective institutions. Determinations of the spiders were made by H. K. Wallace of the University of Florida, to whom we wish to express our thanks.

Activity of males. Large numbers of males were in flight over bare areas and in the surrounding vegetation during the morning hours and lesser numbers during the afternoon. On March 27, 1954, there was considerable cloudiness during part of the day, and during this period little activity was noted. Otherwise sunny weather prevailed, and males were abundant, flying erratically close to the ground, occasionally landing on the ground, and now and then darting after females which were searching for prey or nesting. A few males were found by one of us (KVK) to be attracted to a solution of honey and water which was sprayed on low vegetation. Neither sex was seen visiting flowers; in fact, there are no records known to us of this species ever visiting flowers for nectar.

Hunting and prey transport by females. It was a common sight to see females walking rapidly over the earth with their wings flicking rapidly in the usual manner of pompilids. It is probable that much of the hunting is done in low vegetation and the spiders carried out onto bare places where the female seeks a place to start a nest. At any rate, none was seen attacking spiders, while no less than 27 were found transporting their paralyzed spiders across the bare areas. Twenty-four of these were taken and identified, with the results indicated in the table, while the other three were used for rearing purposes. Sixteen of the twenty-four were a single species of spider, *Lycosa watsoni* Gertsch, all immature. Three others were *L. carrana* Bryant, adult and immature. These species are typical coastal spiders, occurring principally in salt marshes. The four other species used are apparently more wide-ranging. All are ground-dwelling, free-living spiders.

The spiders used varied considerably in size, the smallest measured being 4.6 mm. long (carried by a wasp 7.1 mm. long) and the largest 11.7 mm. long (carried by a wasp 9.1 mm. long). In every case observed, regardless of the relative size of wasp and prey, the

method of transportation was the same. The wasp walked backward, grasping the spider with her mandibles by the base of the hind legs, and holding it rather high in the air, so that smaller spiders were clear of the ground and larger spiders tended to drag their legs on the ground. This is the common method of transportation in the Pompilidae, occurring in many species, for example in *Anoplius apiculatus autumnalis* (Banks) (Evans, Lin and Yoshimoto, Jour. New York Ent. Soc. 61: 61-78, 1953). The latter species, however, when carrying a small spider, will often turn around and proceed forward, holding the spider high off the ground, or may

Table 1. List of Spiders used as Prey by *Anoplius fraternus*

Species	Sex or Stage	Number of Records	Note Numbers
LYCOSIDAE			
<i>Lycosa watsoni</i> Gertsch	Immature	16	KVK32554A,B,C,- E,F; 32754A.HEE- 301; 302A; 720A1, A2,B1,B2.CMY- 664A,B,C,D
<i>Lycosa carrana</i> Bryant	Immature Adult ♂	2 1	KVK32554D; 327- 54B.HEE302B
<i>Sosippus floridanus</i> Simon	Immature	2	CMY400, HEE- 720A3
<i>Pardosa longispin-</i> <i>nata</i> Tull.	Adult ♀	1	HEE720B3
SALTICIDAE			
<i>Habronattus</i> sp.	Adult ♀	1	HEE720A4
<i>Pellenes</i> sp.	Adult ♀	1	HEE720A5

actually fly short distances using the same grasp on the spider. In contrast to this, *fraternus* walked backward over the ground in all the 26 examples observed.

Selection of nesting site. After carrying their prey into a suitable area for nesting, the wasps normally deposit their spiders on the ground and undertake a search for holes and crevices. For example, one wasp (CMY, no. 400) carried her spider about 3 meters across a bare space, deposited it on the ground, and explored an area of about 1.5 meters diameter by walking rapidly in a zigzag

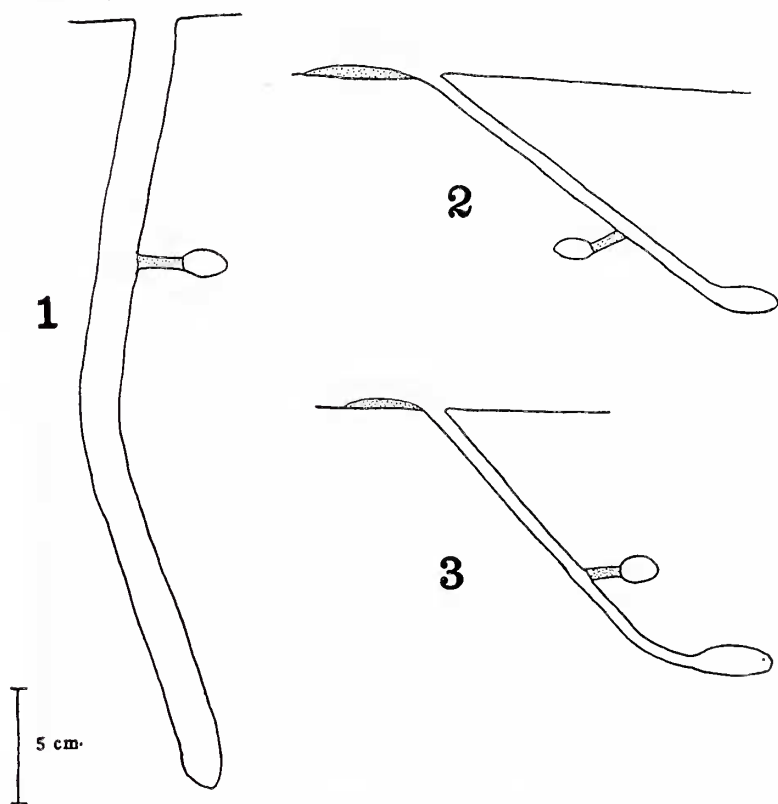
fashion with the antennae in constant motion and the wings flickering rapidly. She encountered some difficulty in finding her spider again, and located it only after about 10 minutes search. After finding it, she picked it up in the usual manner and proceeded another 3-4 meters, when she again deposited it in the midst of a colony of *Bembix cinerea*. After examining two *Bembix* nests in succession for a few moments each, she returned to her prey, again experiencing some difficulty in finding it. She picked up the spider and carried it further, deposited it again, and then stung it two or three times in quick succession. Next, she left it on the earth while she explored further, this time entering a crab-hole which apparently was suitable for nesting. She picked up the spider in the usual manner and carried it directly into the crab-hole. The wasp was first observed at 1126 and the spider was carried into the crab-hole at 1231.

Females of *fraternus* examined depressions and holes of many kinds in their search for suitable nesting places. We did not observe any wasps starting their nests on flat, unbroken earth. One female dug her nest at the lower edge of a heel print in soft soil (KVK, no. 32554 F). Another was at the bottom of a crack in the mud (CMY, no. 660). One specimen (HEE, no. 301) nested on the side of a small vertical burrow, either that of a beetle or a small crab, and another (CMY, no. 400) on the side of a crab-hole about 2 cm. in diameter. Many individuals were seen entering nests of *B. cinerea*, a species which leaves the entrance to its burrow open all through the day. Two specimens (CMY, nos. 668 and 803) nested several centimeters down off the side of *Bembix* burrows. This naturally involved some conflict between the rightful owners of the nest and the trespassers. No. 668 carried her spider into a *Bembix* nest at 1050, and at 1150 was seen carrying small clumps of earth to close the entrance of the *Bembix* burrow. The *Bembix* returned at this time and proceeded to dig this earth away, but the *fraternus* persisted in her efforts, and after several attempts was finally driven away by the *Bembix*. The latter often spend considerable time away from their burrows during the day, and *fraternus* takes advantage of this and apparently often completes its nesting without disturbance. The *Bembix* nest is not harmed in any way by the activities of *fraternus*.

The practice of starting a nest from the side of a depression of some sort is common in the subgenus *Pompilius*, to which *fraternus* belongs. The members of this subgenus have a poorly developed tarsal comb and are not efficient diggers. In this instance there was a relatively hard crust on the mud, and apparently the wasps sought

places where entry could be easily made into the softer soil below.

Nesting activities. These activities could be observed only in the two nests previously mentioned which were started close to the surface of the soil. One of these (KVK, no. 32554F) began her nest at the lower edge of a heel print in soft mud at 1502 on March 25, 1954. Her paralyzed spider, an immature *Lycosa watsoni* Gertsch, was lying on its side on the mud about 40 cm. from the burrow en-



Profiles of nests of *Anoplius (Pompilinus) fraternus* (Banks). Fig. 1—Nest located on the side of a vertical crab hole. Figs. 2 & 3—Nests built from the sides of burrows of *Bembix cinerica* Handlirsch; in each case the lower cell is that of the *Bembix*.

trance. The burrow had a diameter of about 6 mm., and entered the earth at a 45° angle in a southerly direction. The soft mud was pushed out of the burrow into a circular pile about 4 cm. in diameter north of the burrow; small pellets were pushed out of the bur-

row with the posterior legs at intervals of $\frac{1}{2}$ to 1 minute. At 1527 the wasp came out head first, took about a minute to find her spider, then grasped it in the usual manner and walked backward toward the burrow. She deposited it half-way, then took it up again and carried it to the entrance, where it was again deposited. She went in head first, turned around inside the burrow, came to the surface, grasped the spider by the spinnerets and pulled it into the nest abdomen-first at 1529. At 1532 she had not reappeared and the nest was excavated; however there was no egg on the spider. The total length of the burrow and cell was 7.5 cm.

Another wasp (CMY, no. 660) located a favorable place to dig at the bottom of a crack in the mud, about 5 cm. deep, at 1345 on March 24, 1954. About 10 minutes were spent digging the nest, during which time the paralyzed spider was lying on the surface of the mud a short distance away. The wasp made extensive use of the mandibles in digging. She carried the spider in the usual manner into the crack at 1359 and left it beside the entrance while she re-entered the nest for further digging. After about a minute she reappeared, grasped the spider by the spinnerets, and pulled it into the hole. After two minutes, at 1402, she came to the entrance, and used her mandibles to loosen the earth from the walls of the burrow. When she had nearly completed filling the burrow it was noted that she was packing the earth in the burrow with the tip of the abdomen, by moving it up and down slowly while describing more or less of a circle. The wasp completed filling in the nest at 1423, when she was captured and the burrow excavated. The total length of the burrow and cell was only about 4 cm., of which only the outer part of the burrow, about 1.5 cm. long, was filled with a plug of closely packed soil. Since the crack itself was 5 cm. deep, the cell was actually 9 cm. below the surface of the ground. The cell was higher than wide, and the spider was placed in it in a vertical position with the abdomen down. The egg of the wasp was laid diagonally latero-ventrally near the base of the abdomen.

In the case of those nests constructed well down in crab-holes or *Bembix* holes, the details of digging and filling could not be observed. In at least one instance (CMY, no. 400) the wasp carried the spider into a crab-hole backward by the base of the hind legs and presumably deposited it within the hole while the actual nest was dug from the side. This wasp entered the crab-hole at 1231 on March 31, 1953. When the nest was dug out at 1330, the wasp was just finishing the closing of her burrow. The crab-hole had a diameter of about 2 cm. and was a somewhat crooked burrow terminating about 35 cm. down in mud which was saturated with water. The

nest of the wasp was about 10 cm. down the side of this hole. It was about 4 cm. long, with the cell separated from the crab-hole by an earthen plug about 2 cm. long. The cell was longer than high, and the spider lay on its side, with its abdomen away from the earthen plug. The egg of the wasp was laid vertically latero-ventrally about halfway back on the abdomen. The profile of this nest is shown in figure 1.

The two nests prepared off the sides of active burrows of *Bembix cinerea* were of particular interest. One of these wasps (CMY, no. 668) carried her spider directly into a *Bembix* nest at 1050 on March 27, 1954, and was not seen again until 1150, when she appeared to be closing the entrance to the *Bembix* nest. Eventually she was driven off by the returning *Bembix*. When this nest was dug out, the *Bembix* burrow was found to be 16 cm. long, oblique, with the cell 8 cm. beneath the surface. The *fraternus* nest was 12.5 cm. down, off the side of the burrow; there was a plug of earth about 1.5 cm. long separating the more or less spherical cell from the *Bembix* burrow (fig. 2). In the other example (CMY, no. 803), again, about one hour elapsed from the time the *Anoplius* entered the *Bembix* burrow until she emerged. In this instance the *Anoplius* nest was 9 cm. down the burrow and the cell about 9 cm. from the surface ventrally; its construction was about the same as the preceding (fig. 3).

In the six nests of *Anoplius* which were dug out, the depth of the cell varied from 7.5 to 10 cm., a rather narrow range. Since the amount of moisture in the soil increased markedly with increased depth, the position of the cell was probably determined by the amount of soil moisture present. The shape of the cell seemed to vary somewhat, and the spider lay either vertically or horizontally in it, but in every case the abdomen was innermost. The egg was always laid latero-ventrally on the abdomen of the spider, either perpendicular or diagonal to the long axis of the spider. The cell was closed in each case by a closely packed plug of earth 1.5-2 cm. long.

Development. In each case where the paralyzed spider was kept alive, it recovered within a few hours and ran about freely. Probably in nature the spider recovers but is unable to escape from the cell. In three cases larvae were reared to maturity in salve tins. Hatching of the egg occurred in about 2 days; the larval stage required either 4 or 5 days. Two of the larvae were preserved as they began to spin; a third one (CMY, no. 660) was allowed to pupate on March 31, and an adult male emerged from this pupa on May 1. The species is undoubtedly multivoltine.

Summary. In most details of behavior *Anoplius* (*Pompilinus*) *fraternus* closely resembles other species of its subgenus. It is relatively unselective as to prey, taking whatever errant spiders are most prevalent in its habitat. In this case 16 of 24 spiders were immature *Lycosa watsoni*, and the other 8 spiders belonged to 3 other species of Lycosidae and 2 species of Salticidae. The wasp carries the spider over the ground, walking backward, employing the grasp common to most *Anoplius* and many other Pompilidae. The wasp starts her nest from some pre-existing break in the surface of the ground, as do most other *Pompilinus*, and the burrow is rather short, the depth of the cell beneath the surface varying from 7.5 to 10 cm. The spider recovers from paralysis within a few hours. The egg stage lasts about 2 days, the larval stage about 5, and about a month is spent in the cocoon.

Like a few other species of *Anoplius*, e. g., *A. (A.) ithaca* (Banks) and *A. (Arachnophroctonus) apiculatus* (Smith), *fraternus* is not known to visit flowers for nectar. Most of the other unusual features of its biology are related to the habitat which the species occupies. It tolerates a high degree of salinity in the soil, and nests in what is best described as "mud" rather than sand. In the area studied, crab-holes, cracks in the mud, and burrows of *Bembix cinerea* were preferred places to nest. The abundance of *cinerea* and the fact that it does not close its burrow during the daylight hours make its burrows particularly suitable for *fraternus*, which apparently is often able to complete its nesting in the *Bembix* burrows without being disturbed by the rightful owners.

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